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An Unusual New Mammal from the Early Eocene of Wyoming

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Abstract

A newly discovered maxillary dentition from the Early Eocene rocks of the Bighorn Basin, Wyoming, is unlike that of any mammal previously known from this intensively collected region. It represents a new genus and species, here named *Alocodon atopum*. The new form bears superficial resemblance to various mammals, but specific features suggest a real relationship only to palaeoanodonts, particularly *Tubulodon taylori*, a form of uncertain family ties, and the epoicotheriid *Pentapassalus pearcei*. The most significant features of the molars are their cylindrical shape, their odd cusp arrangement, and their reduced enamel. Because of its similarity to *Tubulodon*, *Alocodon* is tentatively allocated here to the Epoicotheriidae (Pholidota, Palaeoanodonta). If correctly assigned, it represents the oldest known member of this poorly represented family and the first from the Bighorn Basin.

Introduction

Collecting in the Willwood Formation of the Bighorn Basin in northwestern Wyoming across nearly a hundred years has yielded a wealth of fossils that document the varied and abundant mammalian fauna of Wasatchian (Early Eocene) time; see papers by Cope, Osborn, Wortman, Loomis, Sinclair, Matthew, Granger and Jepsen, among others, cited by Van Houten, 1944, 1945). In 1972, a Yale Peabody Museum expedition directed by E. L. Simons recovered a specimen of an unusual mammal while surface prospecting on the south fork of Elk Creek, Big Horn County,

Wyoming, in upper "Gray Bull" horizons (see discussion of latter term, Gingerich, 1976). This specimen constitutes postcranial fragments associated in a nodule with a right maxilla and several teeth that are wholly unlike any earlier known specimen from the Bighorn Basin area. Comparisons of this specimen with dentitions of a wide variety of fossil and recent mammals have revealed superficial similarities to several diverse groups but probably significant resemblances to only one, the suborder Palaeoanodonta.

Recovery of such a distinctive new mammal from an intensively collected area is instructive, for it serves as a reminder that fossil collecting from a particular geographic region can possibly never document true species diversity. Even so, the Early Eocene faunas of the Bighorn Basin are among the most completely known Early Tertiary mammalian assemblages, and discoveries of such unusual additions to the fauna are not common.

Systematic Paleontology

Class Mammalia

?Order **Pholidota** Weber, 1904

?Suborder **Palaeoanodonta** Matthew, 1918

?Family **Epoicotheriidae** Simpson, 1927

Alocodon, new genus

Type species: *Alocodon atopum*, new and only known species.

Horizon: upper "Gray Bull" beds, Lower Willwood Formation, Early Eocene.

Known Distribution: Bighorn Basin, Wyoming.

Etymology: Greek: *alox*, furrow, and *odontos*, tooth, in reference to the molar configuration.

Diagnosis: Upper molars longer than wide, and uniquely specialized; M¹⁻² with median longitudinal furrow, several cusps arranged in line on lingual and buccal borders of crown, and no enamel on top of crown. M¹ slightly larger than M², both much larger than M³; M³ greatly reduced, single-rooted, with very low bulbous crown. P³ premolariform, with large paracone, rudimentary metacone, small low protocone. P¹⁻² tiny, single-rooted. Canine of moderate size, triangular in section.

***Alocodon atopum*, new species**

Fig. 1, 2, 3.

Holotype: Yale Peabody Museum (YPM) 30790, fragmentary right maxilla with canine, P³, P⁴ (crown damaged), M¹⁻³, and roots of P¹ and P², right premaxilla with alveolus for incisor, and left maxilla with canine, in concretion with possibly associated postcranial bone fragments; collected by Leonard O. Greenfield.

Hypodigm: Holotype only.

Locality: YPM Locality 348, Sect. 33, T50N R94W, Big Horn County, Wyoming.

Etymology: Greek: *atopos*, unusual, strange.

Diagnosis: Only known species of the genus. Measurements given in Table 1.

Table 1.

Measurements (in mm) of teeth of the holotype of *Alocodon atopum*. YPM 30790.

	Length	Breadth
Canine	1.90	1.70
P ¹	0.75*	0.80*
P ²	—	—
P ³	2.00	1.80
P ⁴	—	—
M ¹	2.60	2.35
M ²	2.45	2.30
M ³	1.40	0.80

*Measured in November 1972.
This tooth is now missing.

Description

As noted above, the type maxilla occurs together with many bone fragments in a hard, fist-sized calcareous and iron oxide nodule. Because of the tenacious matrix, the specimen has so far defied significant preparation beyond minor cleaning of P³ and M³. The osseous remains are so badly fractured that further preparation is unlikely to yield any important information. (There is no assurance that the postcranial fragments are from the same animal as the dentition, for similar concretions from the same area sometimes contain remains of several taxa.) Much of the right side of the rostrum and the floor of the palate are present but were crushed during fossilization and details are thus obscured. Consequently, discussion here will be restricted to the dentition.

The upper dental formula of *Alocodon* appears to be I^{1 (+?)} - C¹ - P⁴ - M³. Fragments of the right premaxilla anterior to the canine contain part of the alveolus for a lateral incisor; its root is slightly smaller than that of the canine (see Figs. 1 and 3). Other incisors may have been present, but none are discernible in the somewhat dissociated premaxillary fragments.

The canine has a single massive root which is, like the crown, roughly triangular in cross-section (see Fig. 3). The crown has three surfaces: enameled buccal and posterointernal faces and an anterointernal face lacking enamel. This last surface appears to be somewhat pitted rather than perfectly smooth, and typical wear striations are not visible on it. The enamel is unevenly distributed at the neck of the canine with a greater extent on the buccal than on the lingual side. This fact, together with the absence of enamel on the occlusal surfaces of M¹ and M² (see discussion below) suggests that the anterointernal surface of the canine originally had very thin enamel or none. The canine is of moderate size, protruding ventrally beyond the occlusal plane (see Fig. 1 and 2). The right canine, nearly complete, measures about 2.6 mm in height from the alveolar border to the tip.

An apparent gap between the canine and the first preserved cheek tooth was occupied by



Fig. 1

Crown view of the holotype of *Alocodon atopum*, YPM 30790, stereopair. Approximately $\times 6$.

two tiny single-rooted premolars, now indicated only by indistinct alveoli which are circular in cross-section. When the specimen was first studied by one of us (T.M.B.) in 1972, the crown of P¹ was present, but was later lost. It was simple and bulbous with no cingula or cristae. The shape and outline of the cross-section of the root of P² is like that of P¹, and presumably its crown was similar (see Fig. 3).



Fig. 2
Lateral view of canine of the holotype of *Alocodon atopum*, YPM 30790.

P³ is premolariform and considerably larger than P¹ but is smaller than the molars. It appears to have three roots. A broken root now situated just anterior and slightly external to the tooth is probably its anterobuccal root, displaced by postmortem fracturing of the maxilla. P³ is roughly triangular in occlusal view and is dominated by a high blunt paracone with slight traces of wear on its posterior surface. The diminutive metacone, slightly worn, has more the appearance of a node on the postparacrista than of a distinct cusp. Behind the metacone there is a slightly worn, minute and inconspicuous cusp at the posterolabial corner of the tooth. A low bulbous protocone is present lingually, towards the posterior part of the tooth, making P³ appear to be skewed posterolingually. On the posterior face of the protocone is a broad wear surface. No conules are present on P³. A very faint lingual cingulum is slightly better defined on the anterior face of the P³ protocone, and enamel covers the entire crown.

P⁴ is badly damaged, and nearly all crown detail has been lost. From what remains, this appears to have been a tooth of roughly quadrangular outline smaller than the molars and

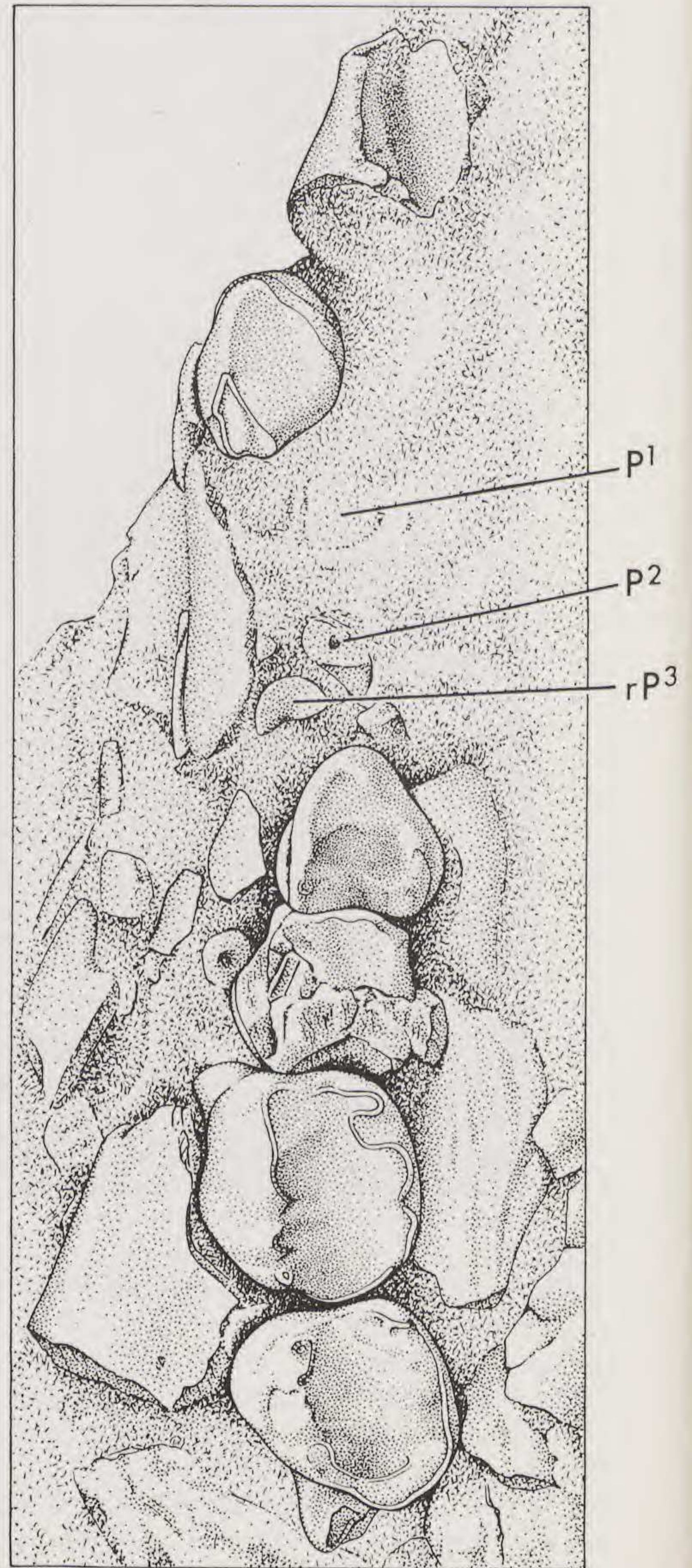


Fig. 3
Crown view of the holotype of *Alocodon atopum*, YPM 30790. Roots of P¹, P² indicated; rP³ is anteriorly displaced root of P³.

slightly larger than P³. Although the crown structure cannot be determined with certainty, a small section remaining at the front of the tooth appears to be more like M¹ than P³.

The molars are the most distinctive teeth. M¹ is the largest and best preserved tooth. It has two labial roots; the presumed lingual root is not visible. In occlusal aspect, it is rectangular and somewhat oval in outline with the long axis oriented anteroposteriorly. The posterior margin of M¹ is convex whereas the anterior margin is marked by an inflection at the midline. The most conspicuous feature of the occlusal surface is the deep longitudinal furrow, devoid of enamel, extending down the anteroposterior midline of the tooth. Cusps are arranged lingually and labially on the periphery of the tooth and the labial cusp series is less peripheral than the lingual row. The tooth is inflated buccally at the base of the crown. The cusps vary in definition and appear more as digitations of the high, crestlike enamel rim bordering the furrow, than as separate cusps. This feature, together with the lack of enamel on top, creates a scalloped pattern of enamel at the periphery of the occlusal surface (see Fig. 1 and 3). Labially there are three cusps, an anterior crestlike one occupying the front half of the crown. Behind the latter cusp and separated from it by a well-defined notch are two smaller cusps, the first is of moderate size and the more posterior one is smaller and lower. The lingual cusps are not as well defined, but consist of a moderate-sized short cusp anteriorly, separated by a broad notch from a rim of enamel occupying the posterior two-thirds of the lingual edge of the tooth. A small indentation in the enamel suggests the former presence of two cusps in this region, but heavy wear has rendered their expression indistinct. The tooth lacks cingula. The enamel on the sides of the crown of M¹ is very thin (approximately 0.1 mm). Obvious wear is confined to the periphery of the crown and there are no distinct wear surfaces or striations on the basined part of the tooth. This appears to indicate that enamel never covered the top of the crown.

M² is slightly smaller than M¹ but is of essentially the same morphology. Its long axis

trends anterolabially-posterolingually. As a result of inflation of the base of the crown anterolabially and reduction of the posterolabial part, the tooth is somewhat tapered posteriorly in occlusal view. In contrast to M¹, M² seems to have only one large labial root. Lingual roots are not visible. The cusps of M² are even less distinct than those of M¹ but are otherwise similar in position and relative size, the only difference being the presence of a minute bulbous cusp anterior to the large anterolabial cusp. M², like M¹, lacks cingula, a styler shelf and enamel on its occlusal surface.

M³ is a diminutive, oval, peglike tooth with a single root. Its crown is bulbous and has a cusplike bulge in the center. A small eroded area on the posterior surface of the cusp seems to be due to fracture rather than wear. Thin enamel covers the crown. M³ is situated well above the occlusal plane of the other cheek teeth and consequently did not occlude with lower teeth. This is probably the original position of M³ (an interpretation supported by the apparent lack of wear). It is situated behind and labial to the midline of M² and abuts against its reduced posterolabial border.

Discussion

Introduction

The right maxillary and premaxillary of *Alocodon atopum* contain at least nine teeth: at least one incisor, a canine, four premolars, and three molars. Since P⁴ may be morphologically similar to M¹, the possibility that there are actually three premolars and four molars, although improbable, cannot be dismissed. Moreover, the molars of *Alocodon* bear some resemblance to those of at least one Early Tertiary group of marsupials (see below).

That *Alocodon* is most likely a eutherian is suggested principally by the structure of P³, the presence of a canine, and the probably eutherian dental formula. Nevertheless, if a eutherian, *Alocodon* is unusual in its peculiarly specialized molars and uncertain cusp

homologies. Many Early Tertiary eutherians have evolved diversely specialized molars (e.g. pantodonts, uinatheres, picrodontids, mesonychids, and taeniodonts), but in most of these the fundamental cusp homologies are more readily perceived.

Thus, the relationships of *Alocodon* are conjectural. We have compared it with a diversity of fossil and recent mammals, and have solicited opinions on the specimen from many vertebrate paleontologists. After comparison with many mammalian groups (outlined below) we believe that *Alocodon* bears significant resemblance only to the palaeonodonts, and especially to *Tubulodon* and *Pen-tapassalus*. Because the dentition of *Alocodon* is so bizarre, however, we present a summary of our comparisons.

Detailed Comparison

The elongate polycuspidate M^{1-2} of *Alocodon* bear a superficial resemblance to those of multituberculates, but possibly resemble the upper premolars of some ptilodontid multituberculates more closely than they do their molars. Furthermore, P^3 of *Alocodon* is tribosphenic (therian-like) and not at all like the P^3 of multituberculates. Retention of the canine, as occurs in *Alocodon*, is unknown in any multituberculate. There is also some resemblance between M^{1-2} of *Alocodon* and teeth of haramiyids, a group known only from the latest Triassic of Europe (see Hahn, 1973). These similarities, however, are surely convergent.

A somewhat closer approximation to the molars of *Alocodon* is seen in the molars of caenolestoid marsupials of the Early Tertiary family Polydolopidae and Middle Tertiary subfamily Abderitinae (Caenolestidae). Polydolopids (see Simpson, 1948; Paula Couto, 1952), are approximately contemporary with *Alocodon* but are known only from South America. Their molars are similarly basined and polycuspidate, but the crowns are often covered with crenulated enamel and the cusps differ in number, form and distribu-

tion from those of *Alocodon*. Where known, the ultimate premolar is enlarged and trenchant (a quite different situation from that in *Alocodon*) and M^1 is similarly modified, though smaller, in at least one genus (*Polydolops*). Although in a majority of polydolopids M^2 is larger than M^3 and M^4 is reduced, only in *Epidolops* is the last molar reduced to such a degree as in *Alocodon*. *Epidolops*, however, contrasts sharply with *Alocodon* in the antemolar dentition (see Paula Couto, 1952). The latter is true also for *Polydolops*, the only other polydolopid in which the antemolar teeth are known. Most of these observations pertain to the Abderitinae as well (see Simpson, 1928). The extreme reduction of the last molar and the lack of specialization of the last upper premolars in *Alocodon* do not strictly rule out affinity with the Caenolestoidea, but they are important contrasts which, when considered along with the fundamental differences in molar structure, are strong evidence against their having close relationship.

Among the pteropodid bats (Megachiroptera) several forms possess elongate upper molars with a median longitudinal furrow. In pteropodids, M^3 and the anterior premolar have been lost, recalling their vestigial state in *Alocodon*. The details of the molar crowns, however, differ markedly from those of *Alocodon*. No well-defined cusps can be distinguished. Although the enamel in the pteropodids *Rousettus* and *Pteropus* is thin, the whole of the labial part of the crown is enameled, unlike the condition of M^{1-2} in *Alocodon*. In pteropodids, the front of M^1 and M^2 is taller than the back, whereas in *Alocodon* the front and back of the cusp rows are more or less of equal height. Megachiropteran dentitions vary considerably between taxa, however, and most forms bear little or no resemblance to *Alocodon*. Further, the available evidence (Russell and Sigé, 1970; Walker, 1969) suggests that megachiropterans differentiated from a generalized chiropteran ancestor sometime after the Early Eocene and before the Early Miocene. The oldest known

megachiropteran, the Early Oligocene *Archaeopteropus*, possessed tuberculate teeth more like those of microchiropterans than megachiropterans. Thus, the occurrence of *Alocodon* in beds as old as the earliest known bats (see Jepsen, 1966) but much older than the earliest known fruit bats (which are and were presumably restricted to the Old World) does not support a possible megachiropteran affinity.

The Palaeonodonta is a rare group of small, Early Tertiary mammals that possess a prominent canine and very modified cylindrical cheek teeth in which the enamel is reduced or absent. These derived features also apply to *Alocodon*, and suggest that it may be related to the Palaeonodonta. In most palaeonodonts, the teeth are reduced to pegs and consequently they bear no other special resemblance to those of *Alocodon*. However, two palaeonodonts, *Pentapassalus* and especially *Tubulodon*, show interesting and probably significant resemblances to *Alocodon*.

Tubulodon taylori is an enigmatic taxon from the late Early Eocene ("Lostcabinian") of the Wind River Basin, Wyoming (Jepsen, 1932). Unfortunately, *Tubulodon* is known only from incomplete lower jaws and cannot be directly compared to *Alocodon*; nevertheless, its lower teeth have features in common with the upper teeth of *Alocodon* which we believe may be significant.

In *Tubulodon*, as in *Alocodon*, the molars are oval (the long axis trends anteroposteriorly) and possess several poorly-defined cusps arranged marginally. The occlusal surfaces lack enamel, appearing at first glance to be heavily worn but as Jepsen (1932) observed, the teeth are still relatively high-crowned and the cusps remain evident, unlike the condition of heavily-worn teeth. Hence the absence of enamel is apparently the original condition of the teeth. Moreover, wear facets are not distinct and appear only on the enameled edges of the margin of the crown. This is the same general pattern as in *Alocodon*. Where still

visible, the enamel of the molars can be seen to have a scalloped margin, reminiscent of the condition in *Alocodon*.

Alocodon resembles *Tubulodon* in another feature, but one of dubious significance, the presence of microscopic tubules in the teeth (Jepsen, 1932). The presence of tubules in *Tubulodon* was cited by Jepsen as a feature indicative of relationship to the Tubulidentata; however, Colbert (1941) cogently argued that the tubules are unlike those in tubulidentate teeth, and he opposed tubulidentate affinities of *Tubulodon*. In addition, Gazin (1952), reported a new Early Eocene epoicotheriid, *Pentapassalus*, that bears some resemblance to *Tubulodon*, including the presence of tubules. Gazin noted tubules in other similarly preserved specimens from the same area, however, and he concluded that in his specimen the tubules were a postmortem feature with no taxonomic importance. As did Gazin, we have found that tubules like those in *Alocodon* and *Tubulodon* are present in teeth of various small mammals from the Willwood fauna, provided the enamel is light-colored and relatively clear. Rather than a peculiar preservational feature, they may be the dental tubules that are present in teeth of virtually all mammals (Peyer, 1968). Their particular salience in *Tubulodon* and *Alocodon* is probably associated with the characteristic reduction of enamel, a factor which enhances the visibility of the tubules. It probably does not indicate extreme tubular development in these taxa.

The lower teeth of *Tubulodon* are about the same length as the corresponding upper teeth of *Alocodon* but are narrower transversely. It is no surprise that they do not occlude well with those of *Alocodon*. In *Tubulodon*, M_1 and M_2 are subequal and M_3 is single-rooted and reduced, but much less so than in *Alocodon*. M_3 of *Tubulodon* is cusped, like M_{1-2} (Guthrie, 1971), in contrast to the diminutive peglike M^3 of *Alocodon*. *Tubulodon* molars do not have a well-developed longitudinal furrow.

These comparisons present the tantalizing but as yet unprovable possibility that *Alocodon* is related to *Tubulodon*. If they were from the same horizon, it might be tempting to speculate that they could be upper and lower teeth from the same taxon. Despite their similarities, however, the evident morphologic and stratigraphic disparities between them argue against this and justify generic separation.

We turn now to the epoicotheriid *Pentapassalus* from the Lostcabinian of southwestern Wyoming, in which Gazin (1952) saw dental resemblance to *Tubulodon*. *Pentapassalus* is known from both upper and lower teeth and is, therefore, more easily compared with *Alocodon*. It possesses several features reminiscent of *Alocodon*: reduced enamel (lacking on the occlusal surface and thin elsewhere), general form of upper molars (longer than wide), peglike M³, and canine form (triangular in section with the anteromedial face honed and devoid of enamel). In contrast to *Alocodon*, however, the three molars are almost equal in size, with M² slightly longer than M¹, and the canine and M³ are noticeably larger. The occlusal morphology of the upper teeth of *Pentapassalus* differs from that of *Alocodon*. Gazin (1952:39) described the occlusal surfaces as nearly flat with two planes of occlusion meeting at a widely obtuse angle in a low transverse ridge, generally near the middle of the tooth "presenting a faintly gabled appearance somewhat as in armadillos." No cusps are evident, a feature in Gazin's view probably due to wear. Perhaps the differences between *Alocodon* and *Pentapassalus* are accentuated by differences in degree of wear. Indeed, the teeth in *Pentapassalus* are much lower crowned than in *Alocodon* and appear to be heavily worn. Unworn teeth of *Pentapassalus* may have resembled those of *Alocodon* more closely.

To summarize, *Alocodon* appears to be closest to *Tubulodon*, among all taxa examined, and to show some resemblances

to *Pentapassalus*. The affinities of *Tubulodon* remain obscure, but it is best regarded as a palaeanodont, and it has been referred tentatively to the Epoicotheriidae (Simpson, 1959; Emry, 1970), a family transferred to the Pholidota in the latter work. *Alocodon* geologically predates both *Tubulodon* and *Pentapassalus* and, if related to them, it would be the oldest described epoicotheriid.

It is unfortunate that the potential alliance of *Alocodon* and *Tubulodon* to each other or to the Epoicotheriidae does little to elucidate the origin of any of these peculiar mammals. Epoicotheriids may have been derived from an unknown Paleocene palaeanodont (Simpson, 1931) but known forms are precluded from an ancestral position because of their greatly reduced dentitions. The origin of palaeanodonts remains unknown.

The occurrence of *Alocodon* in a fauna as well sampled as that of the "Gray Bull" suggests that our knowledge of the composition of Early Tertiary faunas in the Rocky Mountain region is still far from complete and may be biased by sampling of strata which probably record typical but not inclusive paleoenvironments (see Black, 1967; McKenna, 1972).

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